THE EFFECT OF SELECTION UPON THE SEX–RATIO IN DROSOPHILA AMPELOPHILA.

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It is a well-known fact that sex-ratios in most animals approximate equality. The ratio is seldom one of exact equality, however, and the preponderance may be in favor either of the males or the females. The variation from equality is fairly constant for the species. For man the ratio has been found to be 100 females to 105 males; for the horse, 100 to 98; for the cow, 100 to 107; for the sheep, 100 to 97; for the pig, 100 to 111; for the dove, 100 to 105; and for the hen, 100 to 94. These variations are so constant that they cannot be attributed to chance and they are irregularities for which our present theories of sex determination offer no adequate explanation.

The writer has attempted to determine the sex-ratio of the fruit fly, *Drosophila ampelophila*. The determination was made from three unrelated stocks in which the best possible environmental conditions were provided. All matings were in single pairs. Over 35,000 flies were examined and the ratio was found to be 100 females to 95 males.

Moenkhaus tested the effect of selection upon the sex-ratio of *Drosophila ampelophila* and decided that the sex-ratio in this species is "amenable to selection." If it be true that the relative number of males and females in a strain can be varied by selection, the present theories of sex determination must be somewhat modified. Although this fact would not necessarily disprove the theories of sex determination, it would necessitate the assumption of an hypothesis of selective fertilization or of differential mortality or viability of the determining elements.

In view of the vital bearing of Moenkhaus's findings upon the theories of sex determination, it has been deemed worth while to repeat his work.

[1] Contribution No. 159.

METHODS AND MATERIAL.

The selection experiments were carried out upon three unrelated stocks. The stock for the first experiment was collected in Bloomington, Ind.; for the second, in Saratoga, Ind.; and for the third, in Warsaw, Ind. In the first two cases the experiments were started as soon as the stocks were collected from nature but the Warsaw stock was inbred in the laboratory for about six months before the experiment was started. At all times the greatest care was exercised to prevent contamination. The flies were provided with an abundance of food and care was taken to examine all the offspring of each pair. All matings were single pair matings.

Each experiment was conducted upon the offspring of a single pair of flies, that is, for the first experiment, a virgin female was selected from the Bloomington stock and mated to a brother. From among the offspring of this pair of flies, the parents of the two strains were obtained. The one strain in which there was selection for a relatively high number of females in comparison to the number of males, has been called the "high" strain and the one in which the selection was in the opposite direction, has been called the "low" strain. Before selection was started, a sufficient number of flies were examined to obtain a fair estimate of the sex-ratio of the stock under consideration. Moenkhaus's high and low strains were not offspring of a single pair of flies but were obtained by selecting from nature, pairs which had unusual ratios in the desired direction. Furthermore, he knew nothing of the original sex-ratio of his strains before selection began.

In each generation an attempt was made to examine the offspring of ten pairs in each strain. Unsuccessful matings, usually due to poor food conditions, sometimes prevented this. In each generation, the pair which gave the most extreme ratio in the desired direction was used as the parent of the succeeding generation. At times, technical difficulties prevented the most extreme pair being used and in these cases the next best was used. Pairs showing extreme ratios but producing a small number of offspring were not used. Since it was not possible to know which pair had the most desirable ratio till all of the offspring of all the pairs in a generation were examined, the technique of the

experiment was made somewhat difficult. This might have been overcome by isolating some males and females from each mating and then, after the counts for that generation were completed, mating the offspring of the pair giving the most extreme ratio. This would have prolonged the experiment, so to avoid delay, at about the eighth or ninth day after the young had begun to emerge, fifteen pairs were mated from among the offspring of each mating which was being examined. In this way, by the time one generation was finished, the next was almost ready to begin to emerge. Since ten matings in each strain were examined, this necessitated the mating of about 300 pairs of flies in each generation. A control was also carried in each experiment in which a few hundred flies were examined each generation.

PRELIMINARY EXPERIMENT.

This experiment was to test whether the age of the parents would in any way influence the relative number of males and females produced. Several matings were made and the adults

TABLE I.

Showing Results of Experiment to Test the Effect of Age of Parent Upon the Sex-Ratio.

Culture Number.	Original Mating 1 Day Old.		First Transfer 11 Days Old.		Second Transfer 18 Days Old.		Third Transfer 26 Days Old.		Fourth Transfer 34 Days Old.		Fifth Transfer 42 Days Old.		Sixth Transfer 50 Days Old.		Seventh Transfer 58 Days Old.		Eighth Transfer 62 Days Old.		Totals.	
	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.
$202A_2$.	56	68	112	110	105	111	51	40											324	329
$203A_2$.	93	92	110	128	60	89	126	124	172	152	49	60							610	645
$203A_3$.	156	162	135	150	58	60	78	89	136	123	91	93							654	677
$204A_1$.	232	194	140	146	20	24													392	364
$204A_2$.	223	234	155	156	157	151	115	115											650	656
$204A_3$.	134	128	46	70	38	37													218	235
$205A_2$.	214	202	109	114	86	104	115	110	12	12									536	542
$205A_3$.	187	161	140	130	103	113	114	107											544	511
$206A_1$.	68	58	80	55	75	77	78	76	94	89	72	95	126	118	45	45	10	5	648	618
$206A_2$.	149	152	173	176	79	126	135	106	152	130	34	23							722	713
$206A_3$.	173	164	179	207	141	134	129	162	156	159	183	203	71	91					1032	1120
$207A_1$.	90	87	153	143	81	90	100	100											424	420
$207A_2$.	120	118	129	123	86	83	84	69											419	393

were transferred to new bottles every eight days as long as they both lived. The age of the parents does not influence the sex-ratio as is shown by the results given in Table I.

Selection Experiment I. (Bloomington Stock.)

From a stock of flies collected in Bloomington, a virgin female was selected and mated to a male from the same stock. From the offspring of this pair of flies the high and low strains were started. Before selection was begun, 2,936 flies were examined for sex. The ratio was 1,456 males to 1,480 females, or 1 male to 1.06 females. The ratio here is stated in just the reverse order from the customary form but since Moenkhaus used the reverse order, the ratios in the present discussion will be stated likewise to make the two experiments more comparable. Table II. gives the history of the origin of the high and low strains.

Table II.[1]

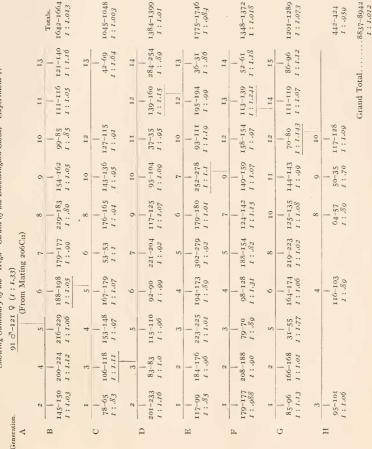*Showing Origin of the "High" and "Low" Strains of the Bloomington Stock.*

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                          206 (Original pair)
                                 |
          206 A₁            206 A₂            206 A₃
            |                 |                 |
          68-58           149-152           173-164

          206 B₁                            206 B₂
            |                                 |
          185-176                           175-166

206 C₃   206 C₄   206 C₅   206 C₇   206 C₈  206 C₁₁   206 C₁₂
  |        |        |        |        |        |         |
15-30    84-74    63-52   108-130   93-100  152-140   91-121
                   Low                                 High
```

Tables III. and IV. give the history of the high and low strains. There is no indication of the ratios having changed in the direction of the selection. In fact, in the high strain where there was selection for a relatively high number of females, the totals show a relatively lower number of females than in the low strain. The totals for the high strain were 8,837 males to 8,942 females or a ratio of 1 male to 1.012 females while in the low strain there were 8,368 males to 9,091 females or a ratio of 1 male to 1.086 females.

[1] In all tables where two numbers are expressed with a dash between them, as 68–58, the number to the left of the dash always represents the male count and the number to the right, the female count.

TABLE III.

Showing Summary of the "High" Strain of the Bloomington Stock. Experiment I.

Generation.

A: 91 ♂–121 ♀ (1 : 1.33) (From Mating 206C₁₂)

Gen.	2	3	4	5	6	7	8	9	10	11	13	Totals.
B	145–150 1:1.03		200–224 1:1.12	216–229 1:1.06	188–198 1:1.05	179–177 1:.99	229–183 1:.80	154–162 1:1.05	99–85 1:.85	111–116 1:1.05	121–140 1:1.16	1642–1664 1:1.013
C	78–65 1:.83	106–118 1:1.11	153–148 1:.97	167–179 1:1.07	92–90 1:.99	53–53 1:1	176–165 1:.94	143–136 1:.95	127–115 1:.91		42–69 1:1.64	1045–1048 1:1.003
D	201–233 1:1.16		83–83 1:1.0	115–110 1:.96			117–125 1:1.07	95–104 1:1.09	37–35 1:.95	139–160 1:1.15	284–254 1:.89	1384–1399 1:1.01
E	117–99 1:.85		184–176 1:.96	223–225 1:1.01	194–173 1:.89	302–279 1:.92	179–180 1:1.01	252–278 1:1.1	93–111 1:1.19	195–194 1:.99	36–31 1:.86	1775–1746 1:.984
F	179–177 1:.988		208–188 1:.90	79–70 1:.89	98–128 1:1.31	188–154 1:.82	124–142 1:1.15	149–159 1:1.07	158–154 1:.97	113–139 1:1.241	52–61 1:1.18	1348–1372 1:1.018
G	85–96 1:1.13		166–168 1:1.01	31–55 1:1.77	164–174 1:1.06	219–223 1:1.02	125–135 1:1.08	144–143 1:.99	70–80 1:1.143	111–119 1:1.07	86–96 1:1.12	1201–1289 1:1.073
H	95–101 1:1.06				116–103 1:.89		64–57 1:.89	50–35 1:.70	117–128 1:1.09			442–424 1:.959

Grand Total........8837–8942 1:1.012

TABLE IV.

Showing Summary of the "Low" Strain of the Bloomington Stock. Experiment I.

$$\frac{63\ \male - 52\ \female}{(1 : .83)}\ \text{(From Mating 206C}_6\text{)}$$

Generation	1	3	4	5	7	8	9	10				Totals
A												
B	164–228 1:1.39	227–248 1:1.09	190–113 1:1.04	138–146 1:1.06	190–187 1:.98	35–88 1:2.51	185–184 1:.99	191–197 1:1.03				1239–1391 1:1.123
C	123–135 1:1.1	51–53 1:1.04	201–327 1:1.12	105–119 1:1.13	120–114 1:.05	60–44 1:.73	176–181 1:1.03	52–71 1:1.37				978–1044 1:1.067
D	175–207 1:1.18	153–128 1:.84	136–160 1:1.18	130–126 1:.97	133–158 1:1.19	192–196 1:1.03	85–104 1:1.22	225–261 1:1.16	135–158 1:1.17 (13)	181–199 1:1.2 (15)		1545–1697 1:1.098
E	176–141 1:.8	125–123 1:.98	138–131 1:.95	141–135 1:.96	151–151 1:1	130–142 1:1.02	285–277 1:.97	167–141 1:.84	193–234 1:1.21 (13)	180–180 1:1 (15)		1695–1655 1:.976
F	275–252 1:.92	174–167 1:.96	145–179 1:1.23	115–105 1:.91	173–190 1:1.10	194–180 1:.93	164–264 1:1.61	246–266 1:1.08	219–215 1:.981 (13)	181–202 1:1.11 (15)		1886–2020 1:1.071
G	114–134 1:1.18		84–180 1:2.14		89–83 1:.93	205–190 1:.93	37–30 1:.81	84–132 1:1.57				613–749 1:1.221
H	52–64 1:1.23	56–72 1:1.29	59–87 1:1.47	48–70 1:1.46	38–47 1:1.24	47–53 1:1.13	8–14 1:1.75	9–9 1:1	45–61 1:1.36 (14)	50–58 1:1.16 (17)		412–535 1:1.208

Grand Total 8368–9091   1:1.086

Selection Experiment II. (Saratoga Stock.)

In the first experiment, a much larger number of flies were examined than were examined by Moenkhaus. But since opposite results were obtained, a criticism might be offered that the writer, by chance, selected a stock which was not affected by selection. So the second experiment was made upon a new and unrelated stock. This stock was collected at Saratoga, Indiana. Fifty matings were made from among the offspring of a single pair. The extremes of these fifty were used as parents of the high and low strains. The counts of these fifty pairs are given in Table V. There were 21,019 flies examined before selection began and the stock showed a ratio of 1 : 1.0512, or 10, 247 males to 10,772 females.

TABLE V.

Showing the Origin of the "High" and "Low" Strains of the Saratoga Stock.

♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.
264	235[1]	202	222	252	241	213	248	179	149
157	165	246	236	157	190	187	168	266	263
208	230	290	280	163	202	241	235	224	234
285	256	192	232	214	237	232	257	109	129
137	160	218	223	176	188	245	205	184	171
173	190	187	217	243	282	75	106	226	206
193	187	251	222	160	189	245	225	195	233
155	168	192	207	200	280	188	171	183	168
252	236	181	307[2]	212	275	129	175	226	222
288	271	183	187	200	225	235	247	234	220

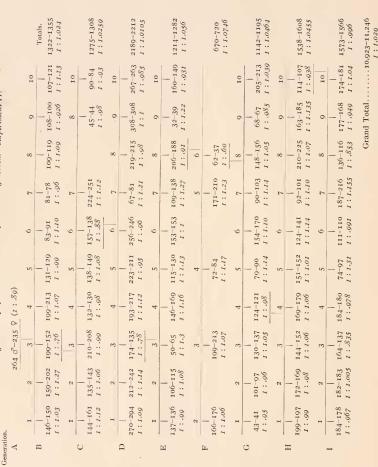Grand Total............................. 10,247 ♂'s to 10,772 ♀'s

The results of the selection in this experiment are given in Tables VI. and VII. In this stock there were greater individual variations from the normal sex-ratios in each direction but they did not breed true. The totals show the high strain to have a higher relative number of females than the low strain. They are as follows: for the high strain, 7,377 males to 8,365 females, or a ratio of 1 : 1.134; for the low strain, 10,923 males to 11,246 females or a ratio of 1 : 1.029. Considering these totals, it might seem that something had been accomplished by selection but when the totals are considered generation by generation the results do not seem so conclusive. If selection has been the factor which

[1] From this mating originated the "low" strain.
[2] From this mating originated the "high" strain.

TABLE VI.

Showing Summary of the "Low" Strain of the Saratoga Stock. Experiment II.

Generation	1	2	3	4	5	6	7	8	9	10	Totals.
A	264 ♂—235 ♀ (1 : .89)										
B	146–150 1:1.03	150–202 1:1.27	199–152 1:.76	199–213 1:1.07	131–129 1:.99	83–91 1:1.10	81–78 1:.96	109–119 1:1.09	108–100 1:.926	107–121 1:1.13	1322–1355 1:1.024
C	144–161 1:1.12	135–143 1:1.06	210–208 1:.99	132–130 1:.98	138–149 1:1.08	157–138 1:.88	224–251 1:1.12	219–215 1:.98	45–44 1:.98	90–84 1:.93	1275–1308 1:1.0259
D	270–294 1:1.09	212–242 1:1.14	174–135 1:.78	193–217 1:1.12	223–211 1:.95	256–246 1:.96	67–81 1:1.21	219–215 1:.98	308–308 1:1	267–263 1:.985	2189–2212 1:1.0105
E	137–136 1:.99	106–115 1:1.08	59–65 1:1.3	146–169 1:1.16	115–130 1:1.13	153–153 1:1	109–138 1:1.27	206–188 1:1.01	32–39 1:1.22	160–149 1:.931	1214–1282 1:1.056
F	166–176 1:1.06		199–213 1:1.07		72–84 1:1.17		171–210 1:1.23	62–37 1:.60			670–720 1:1.0746
G	43–41 1:.95	101–97 1:.96	130–137 1:1.05	124–121 1:.98	79–90 1:1.14	154–170 1:1.10	90–103 1:1.14	148–156 1:1.05	68–67 1:.985	205–213 1:1.039	1142–1195 1:1.0464
H	199–197 1:.99	172–169 1:.98	144–152 1:1.06	169–179 1:1.06	151–152 1:1.01	124–141 1:1.14	92–101 1:1.10	210–225 1:1.07	163–185 1:1.135	114–107 1:.938	1538–1608 1:1.0455
I	184–178 1:.967	182–183 1:1.005	164–137 1:.835	184–180 1:.978	74–97 1:1.31	111–110 1:.991	187–216 1:1.155	136–116 1:.853	177–168 1:.949	174–181 1:1.04	1573–1566 1:.906

Grand Total.......10,923–11,246
1 : 1.020

TABLE VII.

Showing Summary of the "High" Strain of the Saratoga Stock. Experiment II.

Generation	1	2	3	4	5	6	7	8	9	10	Totals.
A				181 ♂–307 ♀ (1 : 1.696)							
B	149–163 I : 1.09	145–152 I : 1.05	147–212 I : 1.442	208–194 I : .932	201–178 I : .885	172–198 I : 1.151	143–149 I : 1.04	240–240 I : 1	22–22 I : 1	207–231 I : 1.116	1634–1739 I : 1.064
C	72–81 I : 1.125		122–109 I : .893		163–158 I : .969	117–118 I : 1.008	106–148 I : 1.306	144–136 I : .944			724–750 I : 1.036
D	171–192 I : 1.123	132–157 I : 1.189	119–203 I : 1.706	189–324 I : 1.714	191–221 I : 1.157	175–212 I : 1.211	140–222 I : 1.586	127–189 I : 1.488	97–169 I : 1.742	136–149 I : 1.096	1477–2038 I : 1.3798
E	107–143 I : 1.34	111–180 I : 1.62	152–144 I : .95	93–109 I : 1.17	88–104 I : 1.18	207–181 I : .874	70–106 I : 1.51	168–228 I : 1.36	98–99 I : 1.01	33–43 I : 1.30	1127–1337 I : 1.186
F	258–276 I : 1.07	50–37 I : .74	118–107 I : .907	119–102 I : .86	260–221 I : .85	81–104 I : 1.284	33–28 I : .85	163–206 I : 1.264		49–56 I : 1.114	1131–1137 I : 1.0053
G	33–84 I : 2.55	82–111 I : 1.35	152–138 I : .91	32–41 I : 1.28	78–94 I : 1.21	42–38 I : .88	27–30 I : 1.11	89–91 I : 1.022			536–627 I : 1.1608
H	74–79 I : 1.068		154–151 I : .9805	108–129 I : 1.10	40–28 I : .70	99–89 I : .899	37–42 I : 1.135				512–518 I : 1.0117
I	63–81 I : 1.28	22–15 I : .68		60–56 I : .93	68–49 I : .72	23–18 I : .78					236–219 I : .928

Grand Total.......7,377–8,365 I : 1.134

has made the difference between the two strains, the difference should be most evident in the later generations of the experiment. This is not true, for a moment's calculation will show that the last three generations in each strain do not show as extreme an average ratio in the desired direction as those which preceed tehm. Although the difference between the totals of the two strains may be sufficiently large to be considered significant, it seems more probable that it is a chance variation, especially since the first experiment showed a similar variation in the direction opposite selection.

SELECTION EXPERIMENT III. (Warsaw Stock.)

In order to make the work still more conclusive, selection was attempted upon a third stock. This stock was collected at Warsaw, Indiana, and kept as a stock culture in the laboratory for about six months before the experiment was started.

Here forty-two pairs were mated from among the offspring of a single pair and the extremes of these matings were used as the parents of the high and low strains.[3] There were 11,190 flies examined before the selection began, 5,448 males to 5,742 females, a ratio of 1 : 1.0539. The counts of these matings are given in Table VIII.

TABLE VIII.

Showing Origin of the "High" and "Low" Strains of the Warsaw Stock.

♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.	♂.	♀.
38	43	91	82	125	106	226	220	255	247
66	72	106	101	155	150	110	114	136	143
133	169	135	156	235	238[2]	80	72	84	77
192	208	41	39	102	105	74	93	94	100
85	75	105	128	48	61	114	129	187	200
147	187[1]	178	189	186	186	195	203	89	79
170	192	91	102	127	142	179	199	175	171
105	113	101	104	187	220	158	156		
125	119	106	114	112	138				

Grand Total............................... 5,448 ♂'s to 5,742 ♀'s

[1] From this mating originated the "high" strain.

[2] From this mating originated the "low" strain.

[3] It will be seen in Table VIII. that the pair used as the parents of the low strain did not produce the most extreme ratio in that direction. This mistake was due to a mathematical error which was not checked up until it was too late to rectify the experiment.

In the latter part of this experiment there was a diveation from the usual methods. The element of time was sacrificed to be able to make a larger number of matings in each generation. A number of males and females were isolated from each mating, being examined, and held to be mated after all of the counts for the generation were finished. By this method it was necessary to make matings only from the cultures which had given the most desirable ratios but in so doing a considerable amount of time was lost between each generation.

This third attempt to modify, by selection, the sex-ratio did not result in bringing about any very significant difference between the two strains. (Tables IX. and X. give the results of selection upon this stock.) The ratios computed from the totals in each strain showed a slight difference in the desired direction but this was so slight that it might be due to chance. Therefore it seems that no definite conclusions can be drawn from this experiment. In the low strain the totals were 9,673 males to 9,951 females, or a ratio of $1:1.0287$ and in the high strain $12,327$ males to $12,898$ females, or a ratio of $1:1.0463$.

Conclusion.

Since three distinct and unrelated stocks of flies show no significant effect of selection, it seems safe to conclude from these data that Moenkhaus's conclusion concerning the amenability of the sex-ratio in *Drosophila ampelophila* will not hold.

Discussion of Moenkhaus's Work.

Moenkhaus concludes from his work on the effect of selection on sex-ratios in *Drosophila ampelophila* that sex-ratios are "strongly transmissible and amenable to the process of selection." From his paper it is somewhat difficult to tell whether Moenkhaus intended to say that he had developed by selection, strains characterized by high and low female ratios or that by selection, he simply maintained a high and low strain which he found in nature. His results are given in the discussion which follows.

By way of explanation it might be said that Moenkhaus called the strain in which he selected for a relatively higher female ratio the "female" strain, and the one in which he selected in

TABLE IX.

Showing Summary of the "Low" Strain of the Warsaw Stock. Experiment III.

235 ♂s = 238 ♀s (1 : 1.013)

Generation.
A

B
- 183–171 1 : .934
- 266–256 1 : .962
- 141–144 1 : 1.02
- 150–155 1 : 1.033
- 112–139 1 : 1.24
- 227–216 1 : .951
- 224–254 1 : 1.13
- 155–125 1 : .806
- Totals: 1458–1460 1 : 1.0013
- (index) 1 … 10

C
- 222–207 1 : .932
- 234–252 1 : 1.077
- 231–242 1 : 1.048
- 105–112 1 : 1.067
- 211–254 1 : 1.204
- 164–193 1 : 1.177
- 247–246 1 : .906
- 158–160 1 : 1.013
- 96–115 1 : 1.198
- 111–109 1 : .982
- Totals: 1779–1890 1 : 1.062
- (index) 1 … 2 3 4 5 6 7 8 9 10

D
- 163–151 1 : .926
- 226–238 1 : 1.053
- 141–153 1 : 1.085
- 139–125 1 : .899
- 206–227 1 : 1.10
- 204–209 1 : 1.025
- 200–297 1 : 1.49
- 142–177 1 : 1.246
- 193–187 1 : .969
- 188–196 1 : 1.04
- Totals: 1802–1960 1 : 1.087
- (index) 1 … 2 3 4 5 6 7 8 9 10

E
- 51–46 1 : .902
- 96–111 1 : 1.156
- 37–45 1 : 1.216
- 125–119 1 : .952
- 84–89 1 : 1.059
- 56–48 1 : .857
- 101–101 1 : 1
- 73–68 1 : .93
- (index) 9 10 11 12 13 14 15 8

E
- 88–92 1 : 1.045
- 101–112 1 : 1.109
- 86–78 1 : .907
- 88–86 1 : .077
- 71–94 1 : 1.324
- 63–84 1 : 1.33
- 53–62 1 : 1.169
- Totals: 1173–1235 1 : 1.053
- (index) 9 10 11 12 13 14 15

F
- 151–123 1 : .815
- 100–72 1 : .72
- 192–158 1 : .823
- 135–152 1 : 1.126
- 113–96 1 : .849
- 121–110 1 : .909
- 117–129 1 : 1.102
- 41–32 1 : .78
- 97–80 1 : .83
- 99–123 1 : 1.242
- (index) 12 3 4 5 6 7 8 9 10 11

F
- 95–123 1 : 1.295
- 154–153 1 : .99
- 44–33 1 : .75
- 68–96 1 : 1.41
- 209–202 1 : .966
- 59–57 1 : .97
- 169–189 1 : 1.118
- 70–73 1 : 1.043
- 55–52 1 : .945
- 51–43 1 : .843
- Totals: 2140–2096 1 : .979
- (index) 12 13 14 15 16 17 18 19 20 21

G
- 64–64 1 : 1
- 103–97 1 : .94
- 51–72 1 : 1.41
- 25–27 1 : 1.08
- 28–38 1 : 1.36
- 39–26 1 : .67
- 59–79 1 : 1.34
- 36–34 1 : .94
- 42–27 1 : .64
- 79–83 1 : 1.05
- 33–39 1 : 1.18
- 34–22 1 : .647
- (index) 20 21 22 23 24 25 26 27 28 30 31

G
- 19–37 1 : 1.95
- 55–46 1 : .84
- 29–29 1 : 1
- 88–78 1 : .89
- 34–34 1 : 1
- 89–69 1 : .78
- 104–108 1 : 1.04
- 59–79 1 : 1.34
- 75–79 1 : 1.05
- 65–71 1 : 1.100
- 115–112 1 : .974
- 55–39 1 : .709
- Totals: 1321–1310 1 : .9916
- (index) 20 21 22 23 24 25 26 27 28 30 31

Grand Total.......9673–9951 1 : 1.0287

TABLE X.

Showing Summary of the "High" Strain of the Warsaw Stock. Experiment III.

147 ♂'s–187 ♀'s (1 : 1.272)

Generation	1	2	3	4	5	6	7	8	9	10	Totals
B	126–115, 1:.913	195–210, 1:1.08	52–42, 1:.81	53–76, 1:1.43	119–127, 1:1.07	138–143, 1:1.04	191–188, 1:.98	194–196, 1:1.01	206–189, 1:.92	208–253, 1:1.22	1482–1539, 1:1.039
C	76–95, 1:1.25	168–202, 1:1.20	209–204, 1:.98	80–85, 1:1.06	228–242, 1:1.06	59–66, 1:1.12	154–170, 1:1.10	183–176, 1:.962	160–179, 1:1.12	181–149, 1:.82	1498–1568, 1:1.047
D	43–43, 1:1	69–78, 1:1.13	79–90, 1:1.14	141–152, 1:1.08	149–141, 1:.946	147–139, 1:.946	194–190, 1:.979	195–202, 1:1.04	193–181, 1:.94	146–152, 1:1.04	1356–1368, 1:1.009
E	28–39, 1:1.39	36–41, 1:1.14	74–93, 1:1.26	59–70, 1:1.19	112–116, 1:1.04	123–128, 1:1.04	107–121, 1:1.13	94–91, 1:.97			
E	92–105, 1:1.14	52–62, 1:1.19	84–82, 1:.976	67–121, 1:1.866	105–126, 1:1.2						1033–1105, 1:1.157
F	145–146, 1:1.007	214–245, 1:1.15	249–246, 1:.988	28–65, 1:2.32	168–179, 1:1.07	169–162, 1:.96	154–162, 1:1.05	77–63, 1:.82	133–146, 1:1.098	79–74, 1:.94	

TABLE X.—Continued.

F

11	12	13	14	15	16	17	18	19	20
100-102	214-228	195-226	182-190	177-149	208-214	194-207	121-135	148-157	93-86
1 : 1.02	1 : 1.07	1 : 1.16	1 : 1.09	1 : .842	1 : 1.03	1 : 1.07	1 : 1.12	1 : 1.06	1 : .93

F

21	22	23	24	25	26	27	28	
132-127	75-98	115-149	114-122	192-206	113-130	118-136	173-156	4080-4315
1 : .96	1 : 1.31	1 : 1.3	1 : 1.07	1 : 1.07	1 : 1.15	1 : 1.15	1 : .902	1 : 1.0576

G

1	2	3	4	5	6	7	8	9	10	11	12
57-69	58-56	85-91	49-56	33-27	84-72	26-46	44-49	44-49	90-94	112-122	92-83
1 : 1.21	1 : .97	1 : 1.07	1 : 1.14	1 : .82	1 : .86	1 : 1.77	1 : 1.11	1 : 1.11	1 : 1.04	1 : 1.09	1 : .90

G

13	14	15	16	17	18	19	20	21	22	23
65-67	46-51	128-109	73-75	53-49	73-86	41-44	62-49	34-32	68-76	
1 : 1.03	1 : 1.11	1 : .85	1 : 1.03	1 : .93	1 : 1.18	1 : 1.08	1 : .79	1 : .94	1 : 1.12	

G

24	25	26	27	28	29	30	31	32	33	34
		80-69	53-33	52-62	134-108	42-35	50-48	49-39	103-113	
		1 : .86	1 : .62	1 : 1.19	1 : .81	1 : .83	1 : .96	1 : .796	1 : 1.097	

G

35	36	37	38	39	40	41	42	43	44	45
113-109	39-60	84-94	32-27	29-32	60-50	61-64	27-36	67-70	152-126	
1 : .97	1 : 1.54	1 : 1.12	1 : .84	1 : 1.10	1 : .83	1 : 1.05	1 : 1.33	1 : 1.05	1 : .829	

2878-2913 1 : 1.0122

Grand Total........12,337-12,898 1 : 1.0463

the opposite direction the "male" strain. This terminology will be used throughout this discussion. As the starting point of his female strain, he selected from nature a pair of flies which produced 52 males and 135 females and in his male strain he started with a pair which produced 84 males and 75 females.

Considering first the effect of selection upon his female strain we find here no conclusive evidence of any progressive change in the direction of the selection. (His data for this strain are given in Table XI.) To be sure, there is a slight increase in the relative number of females in his second and third generations over his first generation, but this fluctuation could easily be attributed to the small number of individuals examined. The greatest difficulty in assuming the effectiveness of selection here, is the fact that his last two generations are the ones in which he obtained the lowest relative number of females. Moenkhaus explains these low ratios of the last two generations in that he possibly made a poor selection in the preceding generation, but if we consider selection as having a cumulative effect (as Moenkhaus seems to consider it) it is difficult to see how one could lose by one poor selection all that he had accomplished in the previous selections. It must be admitted that by using as parents of each succeeding generation, pairs which threw the most extreme ratios in favor of the females, Moenkhaus was able to maintain a strain which on an average gave a relatively high number of females. But this was probably not due to any cumulative effect of selection but to the isolation of a peculiar type of female which will be discussed more fully later.

As to the male strain (Table XII.), Moenkhaus admits that the effect of his selection here has been slight and after examining his data carefully it is difficult to see how it could be assumed that there has been even a slight effect of selection. He started with a ratio (84 males to 75 females) which was only slightly different from normal and this slight difference was not transmitted to the first generation nor any succeeding one. So it seems that he had here a normal strain which would have given the same ratio regardless of the direction of the selection.

The female strain is the unusual one and is in need of an explanation. It throws some very exceptional ratios in favor of

Table XI.

History of Moenkhaus's "Female" Strain.

206 (52 ♂'s : 135 ♀s)

Generation	1	2	3	4	5	6	7	8	9	10	11	Totals
1	21–37	42–68	71–164	76–71	108–125	51–80	43–67	51–46	53–103	8–56	55–102	578–969 / 1 : 1.67
2						7 / 21–49	8 / 41–94	9 / 55–70	10 / 98–178			215–301 / 1 : 1.82
3				3 / 15–37	4 / 18–54	5 / 25–37	7 / 35–71					93–201 / 1 : 2.17
4	1 / 26–47	2 / 39–56	3 / 33–52	5 / 64–67	7 / 53–93	8 / 85–162	10 / 54–106					354–483 / 1 : 1.36
5					4 / 121–139	5 / 32–32	6 / 93–101	7 / 40–114	8 / 86–132			372–518 / 1 : 1.39
5	2 / 51–44	3 / 67–53	5 / 41–47	6 / 74–78	7 / 120–130	10 / 102–136	13 / 41–47					496–535 / 1 : 1.07

TABLE XII.

History of Moenkhaus's "Male" Strain.

207 (84 ♂s : 75 ♀s)

Generation	1	2	3	4	5	6	7	8	9	10	11	Totals
1		79–68			99–121	71–88	67–73	60–57		72–71	86–100	536–579 / 1 : 1.08
2			44–50		133–140		25–21		18–21			220–223 / 1 : 1.00
3	71–98	115–101	76–84	51–73	42–37	45–48	36–39	61–52	84–108			581–640 / 1 : 1.10
4	10–14				41–41	38–38	45–47					142–147 / 1 : 1.04
5	40–32		45–144		46–35	26–26	146–144	72–98	64–74		79–84	518–607 / 1 : 1.17
6	30–50	94–116		58–67	32–51		55–75	85–92	64–104	43–99		561–654 / 1 : 1.42
6	118–109	99–107	104–198	141–157	61–85	56–63	24–27	116–109	42–40	73–67	50–35	944–997 / 1 : 1.05

the females and these exceptional individual ratios caused the relative number of females in the female strain to be higher than normal. These unusual ratios can be readily explained by assuming that the female which Moenkhaus selected as the mother of his female strain carried a recessive sex-linked lethal factor and it will be pointed out later that all of Moenkhaus's data substantiate, very precisely, this assumption. The existence of such factors has been conclusively demonstrated by the recent work of Morgan and his students. A recessive lethal factor is any factor that brings about the death of the individual in which it occurs, provided its effect is not counteracted by the action of its normal allelomorph. Then if a lethal is sex-linked, all males which get it will die for they cannot carry its normal allelomorph since they possess but one X-chromosome. Since all males receiving the lethal factor die, this factor is never transmitted by the male and as a consequence the female can never be homozygous for it. Therefore the lethal factor has no effect on the female but she, by transmitting it to half of her sons, causes their death. Since half of the males die, a 2:1 ratio will result. A female carrying a lethal will transmit it to half of her daughters and they will always be heterozygous for it since they cannot receive it from their father.

Then the female which Moenkhaus used as the mother of his female line was probably a lethal female. It should be said that Moenkhaus is not to be criticised for not considering lethals in his paper, for lethals were not known till two years after his work was published. The original female gave a ratio which was an approximate 2:1 ratio. As mothers of the succeeding generations, Moenkhaus probably selected lethal bearing females (excluding female 5 of generation 4). These females should transmit the lethal factor to half their daughters and this expectation is realized, for from the 31 matings made in the female strain (excluding the offspring of female 5 of generation 4), fifteen 2:1 ratios resulted. Those considered 2:1 ratios are matings 3, 9 and 11 of generation 1; 7, 8 and 10 of generation 2; 3, 4 and 7 of generation 3; 1, 7, 8, and 10 of generation 4; and 7 and 8 of generation 5. So the number of 2:1 ratios obtained would justify the assumption of the presence of a lethal factor.

Another indication of the presence of a lethal factor is the fact that in generation 4, when he used female 5 which gave a normal ratio, as mother of the next generation, all of her daughters also threw normal ratios. This female did not carry the lethal factor and none of her offspring showed abnormal ratios.

A third indication of a lethal factor is the fact that Moenkhaus found in crossing his male and female strains that the female is almost wholly responsible for the transmission of the sex-ratio. For he found if females from a strain possessing a high female ratio be mated with males from a strain possessing a low female ratio or vice versa, the offspring will show a sex-ratio which is wholly or very near that of the strain from which the females were taken. If his female strain carried a lethal factor and if his male strain was a normal strain, as it appears to be, the above result would be the expected one. For, if a lethal bearing female is mated to a normal male, she will transmit the lethal factor to half her daughters but a male from the lethal strain cannot transmit the lethal factor because all of the lethal bearing males die. Therefore the end result would be as Moenkhaus found, that the offspring will show sex-ratios like that of the strains from which the females came.

Of course, the only sure way of testing for a sex-linked lethal factor is to cross the suspected female to a male carrying another sex-linked factor and the resulting F_2 will be characterized by a deficiency in the class of normal males. So it is not possible to determine beyond doubt whether the unusual ratios in Moenkhaus's female strain were due to a lethal factor. But since several lethals have already been found and all of his data substantiate this assumption, it seems that this explanation is probably the correct one.

DISCUSSION.

The writer's three attempts to modify by selection, the sex-ratio in the fruit fly have resulted in no clear-cut evidence that it was modifiable. In each experiment, the work covered more generations and many more individuals than the work of Moenkhaus. Since Moenkhaus's results could not be obtained in any one of the three experiments, it leads one to question Moenkhaus's conclusions or, at least, to question the general application

of his findings. The fact that the difference which Moenkhaus found between his two strains can be readily explained to be due to a cause entirely independent of the cumulative effect of selection, makes his work support, rather than oppose the findings of the writer. It must be admitted that negative results in secletion work can never be conclusive, for the criticism may always be offered that selection over a greater period might have yielded different results. But, nevertheless, we feel justified in concluding from the data here presented that the sex-ratio in *Drosophila ampelophila* is not readily, if at all, modifiable by selection.

LETHALS.

Since the offspring of over 700 pairs of flies were examined for sex in these experiments, and since extreme ratios were sought, it would not be surprising to find a sex-linked lethal mutation. In fact, there is fairly good evidence that one such mutation occurred. This was mating number of 6 generation G of the low strain of the Bloomington stock (Table IV.). This gave an approximate 2:1 ratio (84 males to 180 females). Four matings were made from among the offspring of this mating and three out of the four gave 2 to 1 ratios while the fourth was doubtful. If a sex-linked lethal mutation had occurred, half of the four should have given 2 to 1 ratios and the other half normal. Since so few matings were made, it is possible that all the females chosen were lethal bearers. The stock was lost by accident at this time and further tests were not possible. But since the unusual ratio was transmitted it is probable that a mutation occurred here. In the high series of the Saratoga stock, there were several ratios which approximate a 2 to 1 ratio but none of the flies showing it transmitted this tendency to their offspring. Also in the high strain of the Warsaw stock, generation E mating 12 gave a 2 to 1 ratio. A large number of matings were made among the offspring of this pair but this unusual ratio was not transmitted to any of the progeny.

In all of the matings examined there were comparatively few ratios found which were two to one or more.[1] These extreme

[1] The unusual ratios more frequently occurred where the counts were very small. These cases were considered to have been due to some unfavorable environmental condition.

ratios were more frequently in favor of the females and in only one case was there any evidence that a sex-linked lethal mutation had occurred.

In conclusion, I wish to express my thanks to Professor Fernandus Payne for the suggestion of this problem and also for many helpful suggestions and criticism while the work was in ,progress. I am also greatly indebted to my wife, Elmira Shierling Warren, for help, both in the carrying out of the experiment and in the preparation of the manuscript.

SUMMARY.

1. The sex-ratio in *Drosophila ampelophila* is 100 females to 95 males.

2. The age of the parent has no effect upon the sex-ratio of its offspring.

3. The difference which Moenkhaus found between his two strains, and which he attributed to selection, was probably due to the fact that his male strain was a normal one and his female strain was a lethal bearing one.

4. The sex-ratio in *Drosophila ampelophila* is not readily, if at all, modifiable by selection.

5. There was probably one sex-linked lethal mutation in the writer's selection stocks.

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